Succession of desert plants on debris flow terraces, Grand Canyon, Arizona, U.S.A.

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Vegetation sampling on 11 debris flow terraces in Grand Canyon National Park, Arizona, U.S.A., showed that plant assemblages changed as age of surface increased. The terraces ranged in age from about 5 to about 3100 years. There were distinct differences among sites in the life history characteristics of the dominant plants. Young terraces (5–55 years) were dominated by short-lived plants that had high reproductive potential. Older surfaces were dominated by species with longer life-spans and lower reproductive potential. Density and cover of long-lived species increased with age of surface; for short-lived plants, density was inversely related to surface age. Species composition was also correlated with site age; however, location, exposure, and other factors ensured that no two debris flows supported identical mixtures of species. Succession on recent Grand Canyon debris flows is driven in part by life-history strategies, particularly life-span and seed dispersal traits, and also by climatic factors, especially those that control germination and establishment of the long-lived dominants.

Introduction

During the past three decades, researchers have documented plant succession at a number of locations in the arid south-western United States. Most of these studies examine succession after recent disturbance such as construction (pipeline corridors, power transmission lines), habitation (abandoned townsites), and agriculture (old fields) (Wells, 1961; Vasek *et al.*, 1975*a, b*; Webb & Wilshire, 1979; Karpiscak, 1980; Lathrop & Archbold, 1980*a, b*; Carpenter *et al.*, 1986; Webb *et al.*, 1988). A few studies document succession on undisturbed sites such as debris flows and alluvial terraces that are many thousands of years old (Webb *et al.*, 1987, 1988; McAuliffe, 1991). To date, succession on recent debris flows and alluvial terraces has been little investigated.

In this study, we examined debris flow terraces in Grand Canyon, Arizona, for evidence of plant succession. Debris flows are water-based slurries of poorly sorted material ranging in particle size from clay to boulders (Costa, 1984; Webb *et al.*, 1989).

In Grand Canyon, debris flows begin as failures in bedrock or colluvial slopes during intense precipitation. They can travel anywhere from 1–20 km before reaching the Colorado River (Melis *et al.*, 1995). The debris flow path is marked by deposits of poorly sorted sediment 1–2 m thick; these terraces may be as small as a few square meters or as large as hundreds of square meters (Melis *et al.*, 1995) (Fig. 1).

When they can be accurately dated, debris flow terraces are excellent sites for successional studies. The most recent surfaces are bare of plants. Older terraces can support a dense cover of shrubs and perennial herbs. The youngest and oldest terraces are potential beginning and end points for successional studies. On nearby colluvial slopes, which are remarkably stable, geologically and botanically (Webb, 1996), turnover among dominant long-lived plants is low (Bowers *et al.*, 1995), and the resulting assemblages could be considered climax communities.

As is common in successional studies, we substituted space for time, using 11 surfaces aged 5 to 3100 years to represent a single surface as it might appear during a span of several thousand years. On each surface, we measured cover and density of all perennials in a 50 m × 2 m belt transect. We expected that successional processes would be manifested as consistent, directional trends in species composition, density, cover, and life history strategies. Specifically, short-lived species with high growth rates and reproductive capacity should colonize bare surfaces; with time, longer lived, less fecund species should become increasingly important (Connell & Slatyer, 1977; Vasek, 1979/80; Carpenter *et al.*, 1986; Webb *et al.*, 1988). Cover and density should change as species grow or diminish in importance. With time the heterogeneous species composition of recently formed surfaces should increasingly resemble that of the oldest, undisturbed surfaces (Horn, 1977; Webb *et al.*, 1987).
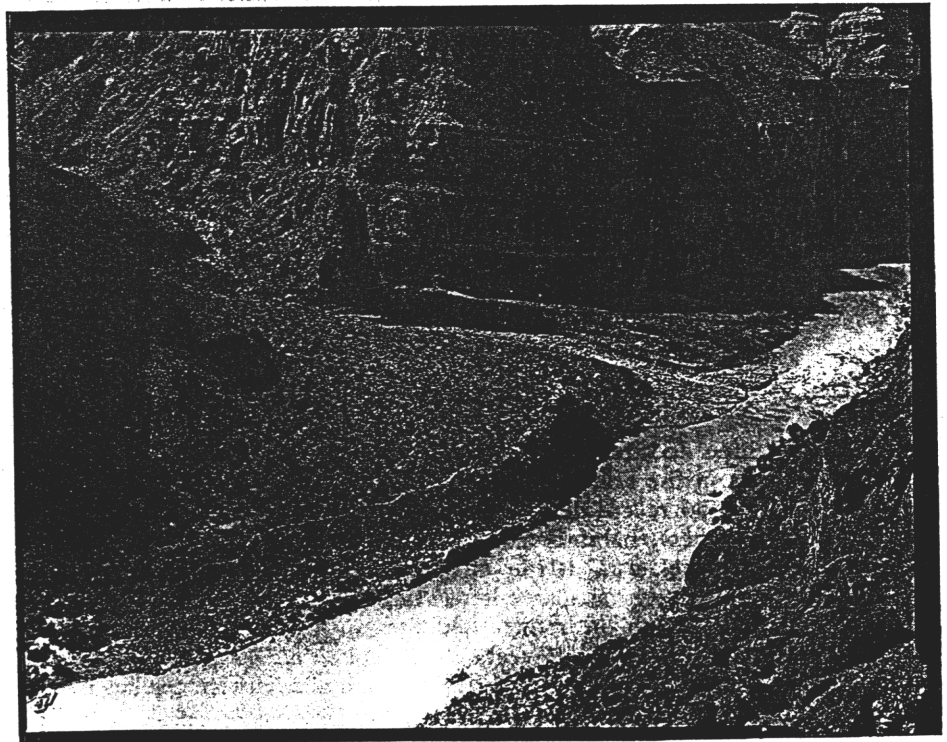

Figure 1. Ancient and modern debris flows at the mouth of Prospect Canyon. The large terrace (left-centre) is about 3100-years-old. The small fan-shaped terrace at river level was formed a few days before the photograph was taken.

Study area

The Grand Canyon of the Colorado River, Arizona, U.S.A., lies between 35°30' and 37° N longitude, and between 111°35' and 113°30' W latitude. The canyon is incised as much as 2000 m into the Colorado plateau, a 336,700 km^2 region centered on the adjoining boundaries of Utah, New Mexico, Arizona, and Colorado (Fig. 2). The study sites were scattered along the 446 km stretch of the Colorado River from Lees Ferry (950 m elevation) to Lake Mead (366 m). At river level, the most common rocks
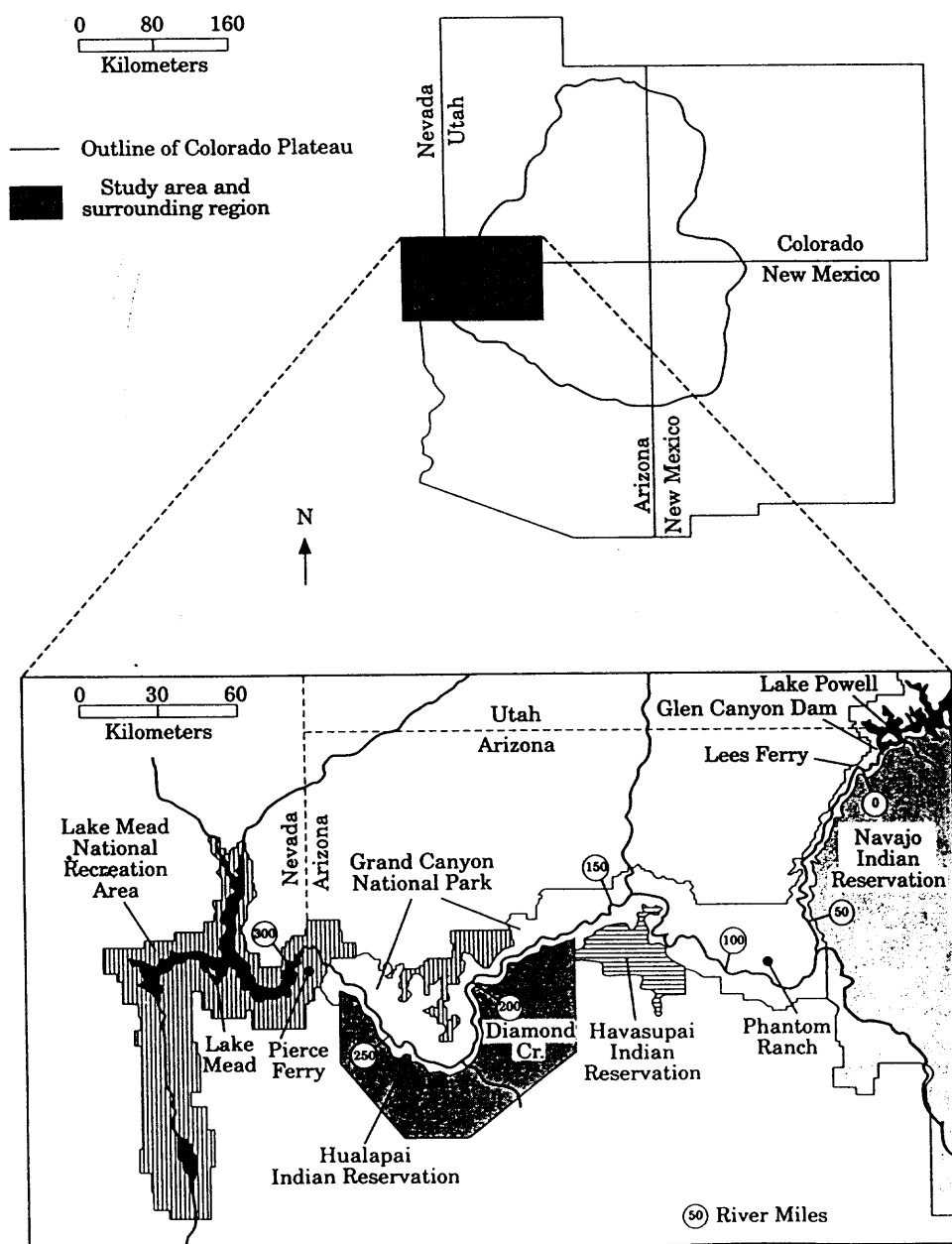

Figure 2. Map of the Grand Canyon region showing locations and features mentioned in text.

are sandstones, shales, and limestones of Cambrian to Permian age (Huntoon *et al.*, 1986). Locally important rocks include Precambrian schist and granite and Quaternary basalt. Sandstones and limestones from the Supai Group, Redwall Limestone, and Muav Limestone are the dominant lithologies in most Grand Canyon debris flows (Melis *et al.*, 1995).

The dates of the debris flows we examined had been previously determined using historical reports (Cooley *et al.*, 1977; Webb *et al.*, 1989); repeat photography (Webb, 1996); and ^{137}Cs, ^{14}C, and ^{3}He dating techniques (Melis *et al.*, 1995) (Table 1). These methods differ in accuracy; whereas historical reports and repeat photography are accurate to specific years, ^{14}C and ^{3}He dating are accurate to ± 60 and ± 500 years, respectively, and ^{137}Cs identifies events as occurring before or after 1952.

Weather stations in Grand Canyon are Phantom Ranch (783 m a.s.l.), Lees Ferry (978 m) and Pierce Ferry (1176 m) (Fig. 2). Annual precipitation along the river corridor ranges from 150–280 mm and is highly variable spatially and temporally (Sellers *et al.*, 1985). Precipitation is biseasonal, with a warm season peak from July through September and a cool season peak from November through March (Sellers *et al.*, 1985). Winter storms originate as large-scale low-pressure frontal systems over the Pacific Ocean. Summer rains, characterized by thunderstorms that usually last several hours or less, result from advection of moist tropical air from the Gulf of Mexico or eastern North Pacific Ocean into Arizona. Winter temperatures at river level are cold as a result of shading by vertical walls and cold air drainage from high plateaus. Along the river corridor, the average daily temperature in January is 2·7°C at Lees Ferry, 7·3°C at Phantom Ranch, and 6·7°C at Pierce Ferry. Summers in Grand Canyon are hot, especially at river level. The average July temperatures are 30·9°C at Lees Ferry, 32·8°C at Phantom Ranch, and 34·6°C at Pierce Ferry (Sellers *et al.*, 1985).

Desert scrub vegetation occurs along the entire length of the Colorado River in Grand Canyon from near river level to about 1130 m above the river (Warren *et al.*, 1982). Species composition changes with increasing distance downstream from Lees Ferry (Warren *et al.*, 1982; Phillips *et al.*, 1987). Cold desert plants typical of Great Basin desert scrub (*Atriplex confertifolia* (Torr. & Frém.) Wats., *Coleogyne ramosissima* Torr., *Opuntia erinacea* Engelm. & Bigel., *Oryzopsis hymenoides* (Roem. & Schultes) Ricker) dominate colluvial slopes in the first 98 km. They gradually give way to a mixture of warm desert species typical of the Mojave or Sonoran Deserts, including *Ephedra* spp., *Fouquieria splendens* Engelm., *Encelia farinosa* A. Gray, *Ferocactus cylindraceus* (Engelm.) Orcutt, *Larrea tridentata* (DC.) Cav., *Ambrosia dumosa* (A. Gray) Payne, and *Opuntia basilaris* Engelm. & Bigel. (Phillips *et al.*, 1987). Slope aspect and substrate can be locally important in determining species composition (Warren *et al.*, 1982) as can low temperature, which in turn is influenced by canyon width and aspect.

Methods

Plant community sampling

Our sample sites were selected on the basis of accessibility from the river and availability of age-dating. So far, 90 Grand Canyon debris flows have been dated using historical photographs (Webb, 1996); the ages of another 17 have been pinpointed or constrained with radiocarbon analysis (Melis *et al.*, 1995). Many of the accessible, dated terraces were either too small or too geomorphologically diverse to provide adequate or uniform samples. Two types of sites were avoided: those where plant roots could penetrate to ground-water, and those that had unusual parent material, for example, debris flows containing saline sediments from the Dox Formation. Because the debris flows examined for this study differed little in parent material, we treated

Table 1. *Features of Grand Canyon debris flows examined for this study. 18-Mile Wash, South Canyon and Fossil Canyon #2 were not used in the various analyses. Canyon aspect, river orientation and elevation were ranked from most cool-moist to most hot-dry; the ranked values were added to obtain the site exposure index*

Site	River mile	Age (years)	Method of age determination	Site exposure characteristics			Site exposure index
				Aspect	Orientation	Elevation (m)	
Mile 126·9	126·9	5	Observation	ENE	NNE–SSW	617	4
18-Mile Wash	18·0	7	Observation	WNW	NE–SW	914	5
Lava Canyon	65·5	28	Cooley et al., 1977	E	N–S	815	4
Crystal Creek	98·2	28	Cooley et al., 1977	SSW	ESE–WNW	701	4
Unkar Canyon	72·5	32	^{14}C, ^{137}Cs	ENE	N–S	792	4
Souh Canyon	31·6	42	Repeat photographs	SSE	NNE–SSW	876	6
Boucher Canon	96·5	43	Repeat photographs	ENE	NNW–SSE	709	5
205-Mile Canyon	205·0	47	Repeat photographs	WSW	NNW–SSE	457	6
Prospect Canyon #1	179·4	55	Repeat photographs	NNW	NE–SW	511	4
Fossil Canyon #1	125·0	240	^{14}C	E	NNW–SSE	625	6
Fossil Canyon #2	125·0	240	^{14}C	E	NNW–SSE	625	5
209-Mile Canyon	209·0	285	^{14}C	E	NNW–SSE	442	4
Prospect Canyon #2	179·4	485	^{14}C	NNW	NE–SW	511	4
Prospect Canyon #3	179·4	3,100	^{3}He	NNW	NE–SW	511	4

substrate as a controlled variable. We did not determine the dimensions of our debris flows, therefore were not able to control for variation in their spatial extent.

Vegetation on debris flow terraces along the river corridor was sampled in February and March 1993. Belt transects were used to determine perennial plant composition, cover and density on 14 debris flows of known ages. The transects were 50 m × 2 m and were placed to obtain the most representative sample of the vegetation. Because time constraints made extensive sampling impractical, a single 5 m × 2 m transect was used at each site, with two exceptions. In one case, the surface was too small for a full 50 m belt. In the other, we sampled two 50 m × 2 m belts to determine how long it would take. Woody plant cover was measured as canopy intercept along each 50 m line. Woody plant density (number of individuals rooted inside the belt) was determined in 2 m × 2 m quadrats within each belt ($N = 25$)). At one corner of each 2 m × 2 m quadrat, a smaller quadrat 0·25 m^2 was used for estimating cover of perennial herbs and grasses according to the following percentage classes: 0–5, 5–12, 12–25, 25–50, 50–75, 75–95, 95–100. Cover and density of dead woody plants were also recorded. Dead plants were identified to species in 7 of the 14 plots.

Data analysis

Using available literature, all woody plants found on the transects were categorized according to life-span: short-lived (1–30 years), medium-lived (30–70 years), long-lived (> 70 years). For those few species for which no information could be found, probable life-spans were assigned based on life history traits (relative seed number and weight, colonizing ability, and habitat) (e.g. Grime, 1979). Dispersal characteristics were determined on the basis of fruit or seed type. Plumed seeds were considered wind-dispersed; seeds enclosed in fleshy fruits were considered animal-dispersed, as were hard-coated seeds requiring burial for germination; and seeds with no obvious means of aerial or animal transport were considered gravity-dispersed (e.g. Howe & Smallwood, 1982).

An exposure index was determined for each site by ranking it according to canyon aspect (most warm–dry to most cool–moist), river direction (most hours of sunlight to fewest hours of sunlight), and elevation (lowest to highest), then adding the rankings. The higher the index, the warmer and drier the site. Canyon aspects were ranked following Haase (1969). South, south–south-west, and south–south-east aspects (most warm–dry) received a ranking of four. North, north–north-west, north-east, and north–north-east aspects (most cool–moist) received a ranking of one. The east, east–north-east, east–south-east and south-east aspects received a ranking of three; the west, north-west, west–south-west, and west–north-west aspects received a ranking of two. A river orientation of east–west was considered to receive the most hours of sunlight (ranking of three), a north–south orientation the fewest (ranking of one). Approximate site elevations and their rankings were: 440–460 m (ranking of five), 510 m (ranking of four), 615–625 m (ranking of three), 700–710 m (ranking of two), and 790–815 m (ranking of one).

Two ordination techniques were used to assess species similarity among sites. A woody species similarity matrix was calculated using a variant of Sorensen's Index (Gauch & Whittaker, 1972). The matrix was then factored in a principal components analysis (PCA) (varimax rotation). The same similarity values were also plotted in one, two, and three dimensions using multidimensional scaling (MDS). This non-metric ordination technique constructs a configuration of points in space from information about the distances between the points (Kruskal & Carroll, 1969). MDS ordinations are evaluated using a measure called 'stress', which determines badness-of-fit, that is, departure from the ideal monotonically increasing relationship between dissimilarity and distance. The lower the stress, the better the fit (Kendall, 1980).

Linear and multiple regressions were used to evaluate the strength of association between several environmental variables (river-mile location, age of surface, exposure index, elevation) and loadings from the first and second rotated components from the PCA. The x- and y-axis coordinates from the MDS were evaluated similarly.

Discriminant analysis was used to determine the relation between age of surface and a number of vegetational characteristics. Surfaces were classified into four groups according to age: very young (<10 years), young (10–100 years), old (100–1000 years) and very old (>1000 years). The dependent variables were: percent woody plant cover, percent perennial herb cover, mean woody plant cover, mean woody plant density, number of woody plant deaths, number of species, and mean density and mean cover of short-lived, medium-lived, and long-lived species.

Results

Altogether, we sampled 14 different debris flow surfaces ranging in age from 5 years to 3100 years (Melis *et al.*, 1995) (Table 1). We omitted three of the 14 from our data analysis: 18-Mile Wash was noticeably disturbed by campers and proved to have anomalously low density and cover; Fossil Canyon #2 was extremely sandy and unusually poor in woody species; and South Canyon overlapped the riparian zone. These three transects did provide useful qualitative information on species composition and rates of colonization. Percent cover and density for all perennial species recorded on the transects are given in Tables 2 and 3. Life-span classes of woody plants are shown in Table 4.

Both PCA and MDS indicated that species composition of Grand Canyon debris flows changes with time in a more or less orderly fashion. The first rotated component of the PCA explained 30·7% of the total variance but could not be identified. Linear regressions showed that the second rotated component, which explained 25·4% of the total variance, correlated equally well with three different variables: age of surface ($R^2 = 0·464$, $p < 0·03$), river-mile location ($R^2 = 0·438$, $p < 0·03$), and elevation ($R^2 = 0·444$, $p < 0·03$). In multiple regressions, surface age and river mile together explained an even greater proportion of the variance (68%, $p < 0·02$), as did the combination of surface age and elevation (69%, $p < 0·02$). It appears that physical location, expressed in terms of river mile and elevation, is just as important as surface age in determining species composition. Physical location could operate in two different but related ways. The vegetation of nearby colluvial slopes and debris flows is a likely source of seeds and other propagules; simultaneously, the local climate influences which colonizing seeds and propagules will prosper. Debris flows in close proximity are more likely to share local climates and seed sources than those farther apart; species composition evidently varies accordingly. In the MDS, the two-dimensional ordination of sites (Fig. 3), which had a stress of 7·7%, was more readily interpretable than the three-dimensional ordination (stress = 5·1%) and offered more information than the one-dimensional ordination (stress = 27·4%). The x-axis corresponded fairly well to age of surface ($R^2 = 0·426$, $p < 0·03$) (Fig. 3). The correlation between the x-axis coordinates and location along the river corridor was marginally significant ($R^2 = 0·362$, $p = 0·05$), again suggesting that the physical distance between sites controls their floristic similarity to some degree. The y-axis apparently represented site exposure as described above (Table 1) ($R^2 = 0·421$, $p < 0·04$).

Examination of species lists from debris flows of different ages confirms that there is a more or less orderly change in species composition as age of surface increases. Vegetation on the youngest debris flows largely comprised short-lived plants such as *Brickellia longifolia* Wats., *Stephanomeria pauciflora* (Torr.) A. Nels., *Gutierrezia sarothrae* (Pursh) Britton & Rusby, *Encelia frutescens*, *Baccharis emoryi* A. Gray, and

Table 2. *Percent cover of all woody plants and herbaceous perennials recorded on debris flow transects. Nomenclature follows Kearney & Peebles (1965), Lehr (1978), and Lehr & Pinkava (1980)*

	Debris flow site										
	Mile 126·9	Lava Canyon	Crystal Canyon	Unkar Canyon	Boucher Canyon	205-Mile Canyon	Prospect Canyon #1	Fossil Canyon #1	209-Mile Canyon	Prospect Canyon #2	Prospect Canyon #3
Age (years)	5	28	28	32	43	47	55	240	285	485	3100
Species											
Trees, shrubs, subshrubs											
Acacia greggii	0·0	0·7	0·0	0·8	0·1	6·9	0·0	4·2	13·7	19·5	0·0
Atriplex canescens	0·0	1·0	0·0	0·4	0·0	0·0	0·0	0·0	0·0	0·0	0·0
Baccharis sarothroides	0·0	0·0	0·0	0·0	0·0	0·5	0·0	0·0	0·0	0·0	0·0
Bebbia juncea	0·0	0·1	0·0	0·0	1·0	17·7	10·1	0·0	0·0	0·0	0·0
Brickellia longifolia	27·2	0·0	0·8	0·0	0·0	0·0	0·0	0·0	0·0	0·6	0·0
Dyssodia porophylloides	0·0	0·0	0·0	0·0	0·0	0·0	1·6	0·0	0·0	0·0	0·0
Encelia farinosa	0·0	0·0	0·0	0·0	14·1	2·4	0·0	8·1	10·4	0·0	0·0
Encelia frutescens	0·4	0·7	0·0	0·0	0·0	0·0	3·4	0·0	0·0	0·0	0·0
Ephedra nevadensis	0·0	0·0	0·0	2·7	2·9	1·5	0·0	5·2	4·1	11·2	3·4
Eriogonum fasciculatum	0·0	0·0	0·0	0·0	0·0	0·0	0·1	0·0	0·0	0·0	0·0
Galium stellatum	0·0	0·0	0·0	0·0	0·5	0·0	0·0	0·0	0·0	0·7	0·0
Gutierrezia sarothrae	0·2	2·9	0·2	0·1	0·0	0·4	0·0	0·0	0·0	0·0	0·0
Hofmeisteria pluriseta	0·0	0·0	0·0	0·0	0·0	0·0	0·5	0·0	0·0	0·0	0·0
Isocoma acradenius	0·0	2·7	23·7	0·0	1·4	0·8	0·0	0·0	0·0	2·5	19·0
Larrea tridentata	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	6·1	0·0	0·0
Phoradendron californicum	0·0	0·0	0·0	0·0	0·2	0·6	0·0	0·0	0·0	0·0	0·0
Porophyllum gracile	0·0	0·0	0·0	0·0	1·1	0·0	2·5	1·2	0·2	1·2	0·0
Prosopis glandulosa	0·0	0·0	0·0	2·3	0·0	0·0	0·0	0·0	3·6	0·0	0·0
Stephanomeria pauciflora	0·0	0·5	0·0	0·1	0·0	0·0	0·1	0·0	0·0	0·0	0·0
Viguiera deltoidea	0·0	0·0	0·0	0·0	0·0	1·1	0·0	0·0	0·0	0·0	0·0

Table 2. *(continued)*

					Debris flow site						
	Mile 126.9	Lava Canyon	Crystal Canyon	Unkar Canyon	Boucher Canyon	205-Mile Canyon	Prospect Canyon #1	Fossil Canyon #1	209-Mile Canyon	Prospect Canyon #2	Prospect Canyon #3
Age (years)	5	28	28	32	43	47	55	240	285	485	3100
Species											
Cacti, succulents											
Echinocereus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Ferocactus cylindraceus	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.4	1.0
Opuntia basilaris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Opuntia engelmannii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.6
Opuntia erinacea	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.3
Opuntia phaeacantha	0.0	0.0	0.0	0.3	0.0	0.0	0.0	6.8	0.0	0.0	0.0
Opuntia whipplei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Perennial herbs											
Allionia incarnata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Aristida hamulosa	0.0	0.4	0.0	0.6	0.5	0.0	0.1	0.0	0.0	0.0	0.0
Aristida purpurea	0.0	0.0	0.1	0.0	1.0	0.0	0.1	0.0	0.0	0.0	0.0
Artemisia ludoviciana	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bothriochloa barbinodis	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Cassia covesii	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0
Dyssodia pentachaeta	0.0	0.0	0.0	0.9	0.5	0.1	0.0	0.0	0.0	0.0	0.0
Hedeoma nanum	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Heteropogon contortus	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Hilaria rigida	0.1	0.1	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0
Machaeranthera pinnatifida	0.0	0.0	0.0	0.1	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Mirabilis bigelovii	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0
Muhlenbergia porteri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0

Table 2. *(continued)*

					Debris flow site						
	Mile 126·9	Lava Canyon	Crystal Canyon	Unkar Canyon	Boucher Canyon	205-Mile Canyon	Prospect Canyon #1	Fossil Canyon #1	209-Mile Canyon	Prospect Canyon #2	Prospect Canyon #3
Age (years)	5	28	28	32	43	47	55	240	285	485	3100
Species											
Sporobolus cryptandrus	0·0	0·3	1·1	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
Sporobolus flexuosus	0·0	0·0	0·0	0·4	0·1	0·3	0·0	0·5	0·0	0·0	0·0
Stanelya pinnata	0·0	0·1	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
Tridens muticus	0·0	0·0	0·0	0·0	0·1	0·0	0·0	0·0	0·0	0·0	0·0
Tridens pulchellus	0·0	0·1	0·0	0·7	0·7	0·1	0·6	0·0	1·1	0·0	0·0

Table 3. *Density (plants per ha) of all woody plants recorded on debris flow transects. Nomenclature follows Kearney & Peebles (1960), Lehr (1978), and Lehr & Pinkava (1980)*

					Debris flow site						
	Mile 126·9	Lava Canyon	Crystal Canyon	Unkar Canyon	Boucher Canyon	205-Mile Canyon	Prospect Canyon #1	Fossil Canyon #1	209-Mile Canyon	Prospect Canyon #2	Prospect Canyon #3
Age (years)	5	28	28	32	43	47	55	240	285	485	3100
Species											
Trees, shrubs, subshrubs											
Acacia greggii	0	100	0	200	100	400	0	100	200	300	0
Atriplex canescens	100	800	0	200	0	0	0	0	0	0	0
Baccharis sarothroides	0	0	0	0	0	100	0	0	0	0	0
Bebbia juncea	0	100	0	0	400	4800	2100	0	0	0	0
Brickellia coulteri	0	0	0	0	0	0	100	0	0	0	0
Brickellia longifolia	17,200	300	1300	0	0	0	0	0	0	0	0
Dyssodia porophylloides	0	0	0	0	0	0	1000	0	0	1200	900
Encelia farinosa	0	0	0	2800	5000	1000	0	1600	2200	0	0
Encelia frutescens	100	300	0	200	0	0	500	0	0	0	0
Ephedra nevadensis	0	100	0	0	200	200	100	100	400	1000	200
Eriogonum fasciculatum	0	0	0	0	0	0	100	0	0	200	100
Galium stellatum	0	0	0	0	0	0	0	0	0	300	0
Gutierrezia sarothrae	700	4100	300	300	100	400	0	0	100	0	0
Hofmeisteria pluriseta	0	0	0	0	0	0	0	0	0	0	0
Isocoma acradenius	0	800	8400	0	800	200	0	0	0	0	0
Larrea tridentata	0	0	0	0	0	0	0	0	200	100	700
Phoradendron californicum	0	0	0	0	200	0	0	0	200	100	0
Porophyllum gracile	0	0	100	0	2200	400	2400	1600	800	1300	0
Prosopis glandulosa	0	0	500	100	0	0	0	0	0	0	0
Stephanomeria pauciflora	300	300	0	<100	0	0	600	0	0	0	0

Table 3. *(continued)*

Debris flow site

Species	Mile 126·9	Lava Canyon	Crystal Canyon	Unkar Canyon	Boucher Canyon	205-Mile Canyon	Prospect Canyon #1	Fossil Canyon #1	209-Mile Canyon	Prospect Canyon #2	Prospect Canyon #3
Age (years)	5	28	28	32	43	47	55	240	285	485	3100
Thamnosma montana	0	0	100	0	0	0	0	0	0	0	0
Cacti, succulents											
Agave utahensis	0	0	100	0	0	0	100	0	0	0	0
Echinocereus sp.	0	0	0	100	200	0	400	0	200	1300	1000
Ferocactus cylindraceus	0	0	0	0	0	0	200	0	0	100	400
Mammillaria microcarpa	0	0	0	100	1600	0	200	0	500	0	0
Opuntia basilaris	0	0	0	0	0	0	0	0	0	0	3100
Opuntia engelmannii	0	0	0	0	100	0	0	0	0	0	0
Opuntia erinacea	0	100	0	0	0	0	0	0	0	400	0
Opuntia phaeacantha	0	0	0	200	0	0	0	300	0	0	0
Opuntia whipplei	0	0	0	0	0	0	0	0	0	0	100

Table 4. *Maximum observed life-span and seed dispersal characteristics of woody plants found on the transects. Nomenclature follows Kearney & Peebles (1960), Lehr (1978), and Lehr & Pinkava (1980).*

Species	Fruit or seed type	Primary dispersal mode	Life-span (years)	Source (life-span)
Long-lived plants				
Acacia greggii	Capsule	Animal	130	Bowers et al., 1995
Ephedra nevadensis	Cone	Gravity	250	Bowers et al., 1995
Galium stellatum	Nutlet	Animal	100	Bowers et al., 1995
Larrea tridentata	Nutlet	Gravity	>2200	Bowers et al., 1995
Opuntia basilaris	Dry berry	Animal	100*	Bowers et al., 1995
Opuntia erinacea	Dry berry	Animal	100*	Bowers et al., 1995
Opuntia whipplei	Dry berry	Animal	100*	Bowers et al., 1995
Prosopis glandulosa	Capsule	Animal	100	Bowers et al., 1995
Medium-lived plants				
Agave utahensis	Capsule	Gravity	40†	Gentry, 1978
Atriplex canescens	Samara	Wind	70	Bowers et al., 1995
Baccharis sarothroides	Achene	Wind	unknown	Goldberg & Turner, 1986
Brickellia coulteri	Achene	Wind	42	Bowers et al., 1995
Encelia farinosa	Achene	Gravity	37	Bowers et al., 1995
Ferocactus cylindraceus	Berry	Animal	55	
Opuntia engelmannii	Berry	Animal	32*	Goldberg & Turner, 1986
Opuntia phaeacantha	Berry	Animal	32*	Goldberg & Turner, 1986
Thamnosma montana	Capsule	Gravity	medium†	Webb et al., 1988
Short-lived plants				
Bebbia juncea	Achene	Wind	20†	Vasek et al., 1975a
Brickellia longifolia	Achene	Wind	28	This paper
Dyssodia porophylloides	Achene	Wind	unknown	
Echinocereus sp.	Berry	Animal	9	Goldberg & Turner, 1986
Encelia frutescens	Achene	Gravity	unknown	
Eriogonum fasciculatum	Achene	Gravity	20†	Vasek et al., 1975a
Gutierrezia sarothrae	Achene	Wind	20	West et al., 1979

Table 4. (*continued*)

Species	Fruit or seed type	Primary dispersal mode	Life-span (years)	Source (life-span)
Hofmeisteria pluriseta	Achene	Wind	20	Robert H. Webb, unpublished photographs
Isocoma acradenius	Achene	Wind	20‡	Goldberg & Turner, 1986
Mammillaria microcarpa	Berry	Animal	11	Goldberg & Turner, 1986
Phoradendron californicum	Berry	Animal	unknown	
Porophyllum gracile	Achene	Wind	20	Goldberg & Turner, 1986
Stephanomeria pauciflora	Achene	Wind	20†	Vasek *et al.*, 1975b
Viguiera deltoidea	Achene	Gravity	20†	Vasek *et al.*, 1975b

*Clonal reproduction enables certain *Opuntia* spp. to survive for >100 years.
†Longevity estimated rather than observed.
‡Based on *Isocoma tenuisectus*.
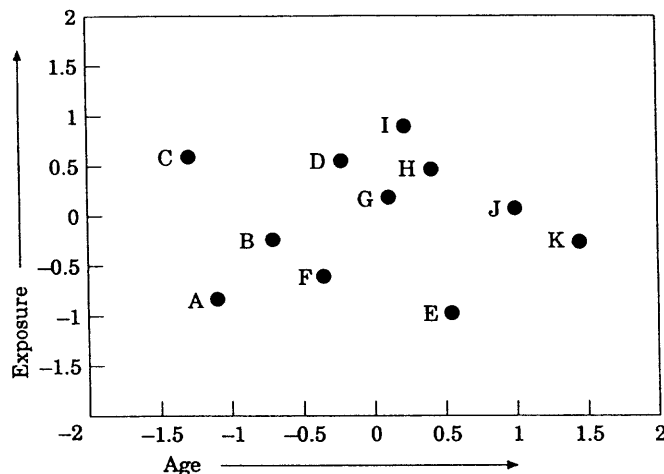
Figure 3. Two-dimensional ordination of species similarities. Dimension 1 represents age, with −2 = youngest and +2 = oldest. Dimension 2 represents site exposure, with −2 = most hot/dry and +2 = most cool/moist. Sites are as follows: (A) Mile 126·9; (B) Lava Canyon; (C) Crystal Creek; (D) 205-Mile Canyon; (E) Prospect Canyon #1; (F) Unkar Canyon; (G) Boucher Canyon; (H) 209-Mile Canyon; (I) Fossil Canyon #1; (J) Prospect Canyon #2; (K) Prospect Canyon #3.

Isocoma acradenius (Greene) Greene. Longer-lived species were generally not as quick to colonize. *Ephedra nevadensis* Wats. occurred on the 7-year-old debris flow but not on the 5-year-old surface. Similarly, *Encelia farinosa, Opuntia engelmannii* Salm-Dyck., *Opuntia phaeacantha* Engelm., *Prosopis glandulosa* Torr. and *Acacia greggii* A. Gray were found on flows as young as 28 years but not as young as 7 years. Some species were found only on very old surfaces. *Larrea tridentata* occurred only on flows ≥ 285 years, for instance, and *Fouquieria splendens* was not observed on any debris flow in the study area, although populations occurred on nearby colluvial slopes. Other successional studies in North American deserts have also reported slow recruitment and late arrival of *Larrea tridentata* (Webb *et al.*, 1988; McAuliffe, 1988, 1991). In some locations, however, *Larrea* seedlings appear early in successional sequences (Shreve, 1929, 1942; Vasek, 1979/80; Martin M. Karpiscak, pers. comm.). Casual observation suggests that, with time, plant assemblages on debris flows increasingly resemble the oldest, most stable plant communities in the area, supporting many of the same species at similar densities and covers.

Density and cover of particular species also show marked trends with time (Tables 2 and 3). On the 5-year-old debris flow, *Brickellia longifolia* had high density (17,200 per ha) and cover (27·2%). Many dead *Brickellia* seedlings (7500 per ha) were found under the canopies of the mature plants. *Brickellia* density and cover were markedly lower on the 7-year-old debris flow, and very few individuals were present on the 28-year-old flow. *Bebbia juncea* reached peak cover and density on the 47-year-old debris flow; this species was not found on flows older than 55 years. *Ephedra* cover and density were relatively low on the younger debris flows and relatively high on older ones. *Acacia greggii* followed a similar pattern. The subshrub *Gutierrezia sarothrae* occurred on surfaces of any age; its density tended to decline from younger to older surfaces.

Because of the small number of debris flows examined, the discriminant analyses should be interpreted with caution. Certain general trends in vegetation are evident. Short-lived species (Table 4) were densest on the youngest surfaces ($F = 9.158$, $p < 0.01$), largely accounting for the inverse relationship between surface age and
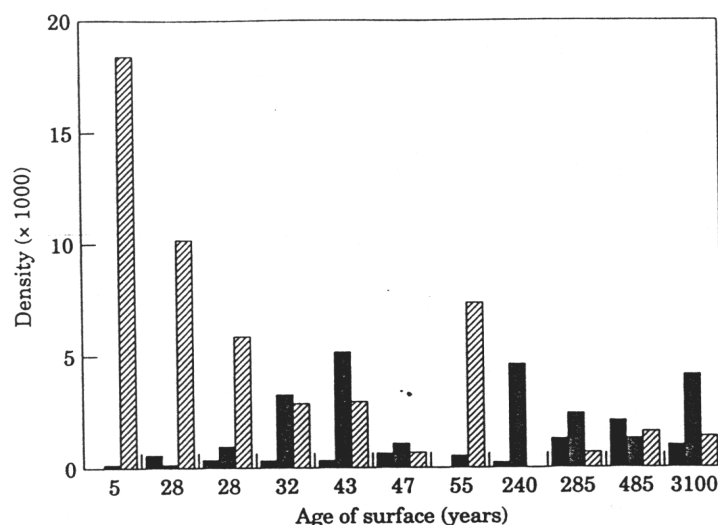
Figure 4. Mean density (number per ha) of long- (■), medium- (▣) and short-lived (▨) woody plants on debris flows of different age.

woody plant density ($F = 8.970$, $p < 0.01$) (Fig. 4). Cover of long-lived species (Table 4) was highest on the oldest surfaces (6.394, $p < 0.03$) (Fig. 5). Number of woody plant deaths was inversely related to surface age ($F = 57.837$, $p < 0.001$), a trend that was strongly influenced by the very high number of *Brickellia longifolia* deaths on the 5-year-old surface. Variables that were not significantly correlated with surface age were mean cover of woody plants, mean cover of medium- and short-lived species, percent cover of woody plants, percent cover by life-span class, mean cover of perennial herbs, density of long-lived and medium-lived species, and species number. Because we sampled at the beginning of the growing season, our values might
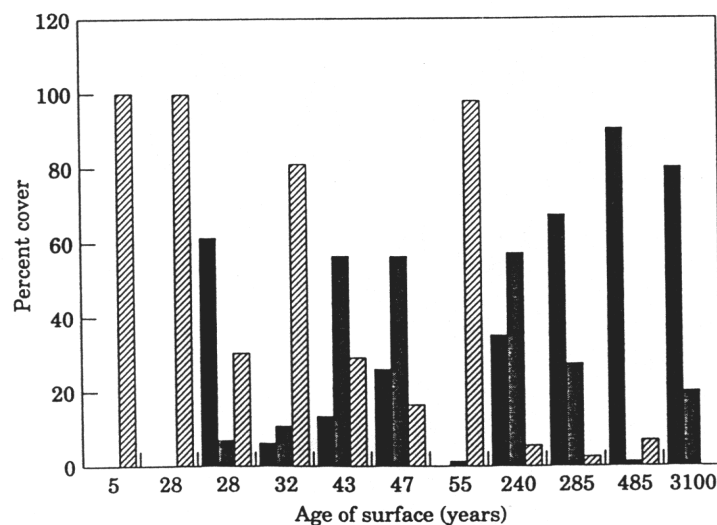
Figure 5. Mean percent cover of long- (■), medium- (■) and short-lived (▨) woody plants on debris flows of different-age.

underestimate the density of perennial herbs and the cover of deciduous shrubs, particularly *Acacia greggii*.

Unlike short-lived species, medium- and long-lived species did not increase in density over time (Fig. 4). This could be an artifact of our small sample size. Alternatively, it could indicate that certain longer-lived species are present rather early (surfaces aged 28–55-years-old) and that over time, they increase greatly in cover but little in density. That percent cover of long-lived species tends to increase with surface age (Fig. 5) indirectly supports the latter hypothesis.

Discussion and conclusions

On Grand Canyon debris flows, the pattern of plant occupation over time resembles successional patterns at other sites in the arid south-western United States (e.g. Vasek, 1979/80; Carpenter *et al.*, 1986). The general pattern is one in which the life history characteristics of a plant community change more predictably over time than its species composition. In Grand Canyon, initial seres are typically dominated by *Brickellia longifolia*, a fast-growing, short-lived shrub. The seedlings evidently cannot establish under the canopies of mature plants, therefore death of the original pioneers signals the end of the sere. During the next sere, from about 28 to 55 years, short-lived shrubs and subshrubs dominate, and seedlings of longer-lived plants establish, forming heterogeneous communities. As the shorter-lived species are replaced by those with longer life-spans, the number of dead plants declines rapidly. From about 55 to 300 years, the trend is toward decreasing representation of short-lived woody plants (although they never disappear altogether), accompanied by increasing dominance of medium- and long-lived species. Once established, these plants tend to occupy sites for many decades or even centuries (Bowers *et al.*, 1995). The same medium- and long-lived species dominate nearby colluvial slopes which are presumably many thousands of years older than the oldest debris flows studied here and could be considered the 'climax' communities for desert vegetation along the river corridor.

Species composition also changes with age of debris flow (Fig. 3). As at other arid sites, however, exactly which species will be present at a given stage is not necessarily predictable, as shown by three debris flows aged 28–32 years: Lava Canyon is fairly similar in species composition to Crystal Creek (similarity = 0·370, distance apart = 52·6 km) and to Unkar Canyon (similarity = 0·452, distance apart = 11·3 km), but Crystal Creek and Unkar Canyon are quite different (similarity = 0·154, distance apart = 41·4 km). Clearly, factors other than age also control species composition. As discussed above, location and site exposure strongly influence which species will colonize a site and which of those colonizers will survive. Other factors that might influence species composition include debris flow size, predation, soil texture, post-depositional flooding, and climatic perturbations.

Our sample size was too small for meaningful tests of the various successional mechanisms proposed by Connell & Slatyer (1977), Grime (1979), Tilman (1988), Stevens (1989), and others. The most important mechanisms in Grand Canyon are likely to be life history traits such as life-span, seed production, and seed dispersability. Theoretically, pioneering shrubs produce numerous, lightweight seeds and die out within two or three generations; meanwhile, longer-lived plants, which typically produce fewer, heavier seeds, become established and occupy their sites for decades or even centuries. In our study, more than half of the short-lived species have seeds primarily dispersed by wind compared with none (or possibly only one) of the long-lived species (Table 4). The proportion of animal-dispersed seeds is highest among long-lived plants (75% of woody species on the transects) and lowest among short-lived plants (21%) (Table 4). The rodents and ants that transport and bury seeds of *Ferocactus, Opuntia, Acacia* and *Prosopis* have limited foraging ranges: less than 100 m

for *Neotoma*, for example (Finley, 1990), and about 10–24 m for *Pogonomyrmex* or *Veromessor* (Carroll & Janzen, 1973). Seeds transported by wind can theoretically travel distances that exceed these ranges by several orders of magnitude (Sheldon & Burrows, 1973), arriving on newly deposited surfaces well before most animal-transported seeds. Moreover, granivores are unlikely to frequent a terrace until their food plants are established and producing seed. For these reasons, establishment of animal-dispersed/long-lived plants is likely to lag behind that of wind-dispersed/short-lived plants.

Although we cannot rule out the possibility that some colonizers arise *in situ*, it seems unlikely that a newly deposited debris flow has a significant seed bank. The lightweight, fragile seeds typical of early successional species are unlikely to survive the churning and grinding that occurs when many tons of rock are mobilized in slurry of gravel and mud. Heavier seeds might survive, but there is only a small chance that they would be buried at the proper depth for germination and emergence.

In arid environments, soil development may be an important mechanism in regulating succession on ancient debris flow terraces, but debris flows younger than about 1000 years have not had sufficient time for significant soil development (Birkeland, 1984). One edaphic factor that might regulate plant succession on Grand Canyon debris flows is cryptogamic soil crusts. The younger terraces lacked soil crusts, which evidently develop some time after 55 years and before 285 years. Cryptogamic crusts play an important role in arid ecosystems by fixing nitrogen, stabilizing soils, improving plant nutrient status, and increasing soil moisture retention (Belnap, 1993; Belnap & Gardner, 1993), traits that might well affect plant succession on Grand Canyon debris flows. For example, if early successional species tolerate low soil nitrogen, they could colonize a debris flow before soil crusts develop. After soil crusts have formed, later successional species that have higher nitrogen requirements could become established, then attain dominance by virtue of longer life.

Climatic factors may also influence successional processes in Grand Canyon. Germination and emergence of woody desert plants often depend upon a favorable combination of temperature and moisture conditions (Shreve, 1917; Barbour, 1968; Sheps, 1973; Ackerman, 1979; Sherbrooke, 1989). These may be relatively frequent, as for *Encelia farinosa*, or relatively infrequent, as for *Fouquieria splendens* and *Larrea tridentata* (Barbour, 1968; Bowers, 1994). On Grand Canyon debris flows, prolonged unfavorable conditions for regeneration would delay the establishment of long-lived species, especially those with precise and rarely met requirements for germination. The patterns of species turnover seen in this study, therefore, may be specific to the particular climate that has prevailed in Grand Canyon during the last 300 years or even unique to individual sites as a result of anomalous frost, drought, or rainfall events. Similarly, in Death Valley the time required for full recovery after disturbance might exceed past periods of climatic stability (Webb *et al.*, 1987).

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